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The  
Development of Glyphioceras and the  
Phylogeny of the Glyphioceratidæ.

BY  
JAMES PERRIN SMITH.

WITH THREE PLATES.

*Issued October 16, 1897.*

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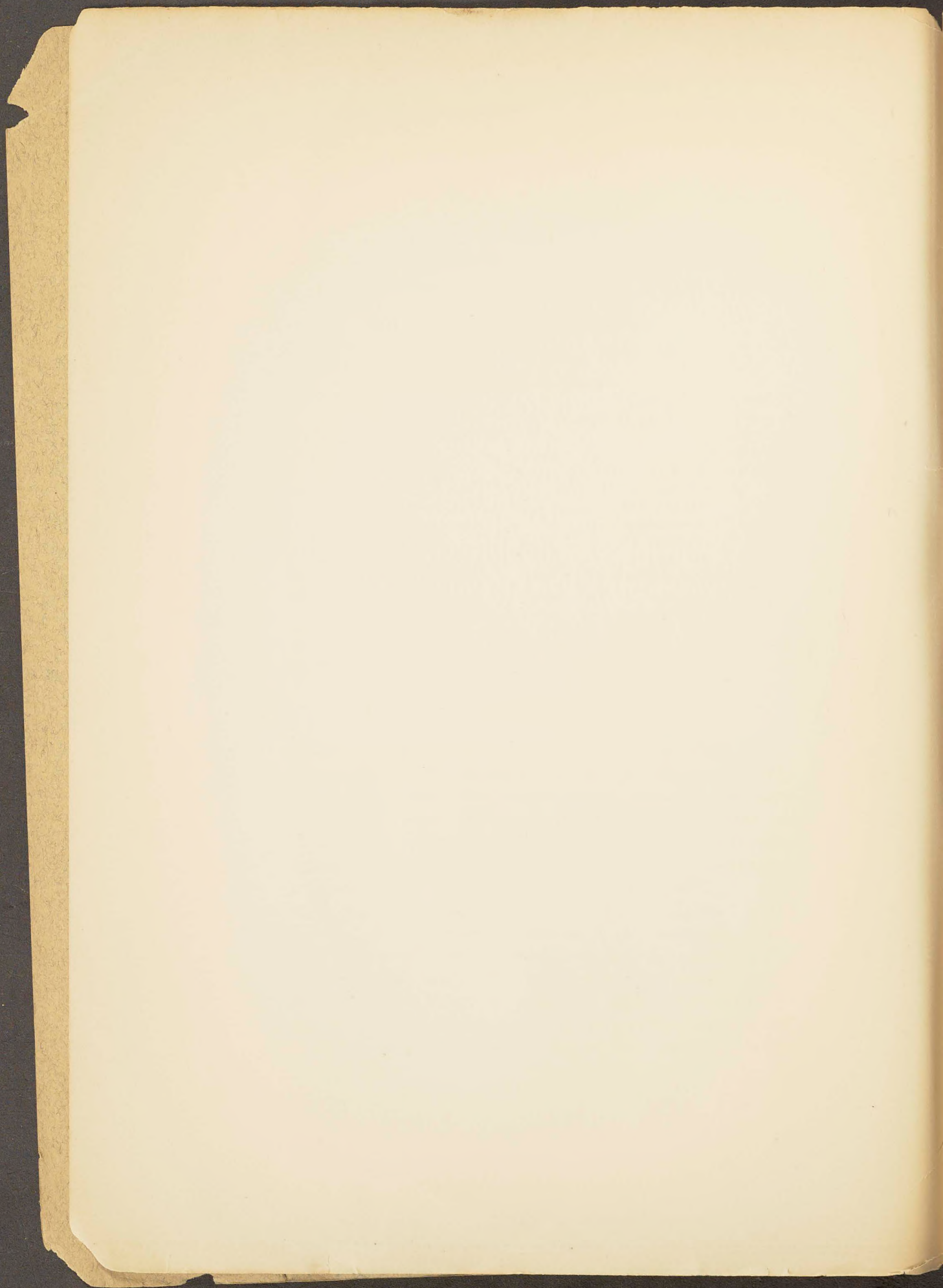
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# THE DEVELOPMENT OF GLYPHIOCERAS AND THE PHYLOGENY OF THE GLYPHIOCERATIDÆ.

BY JAMES PERRIN SMITH.

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## INTRODUCTION.

ALL modern classification is intended to be genetic, but in reality is usually not so, being based not on ontogenetic study, but rather on a comparison of supposed genetic series of adults. Much that has passed for demonstration has been in fact only conjecture. The only safe way is comparative study of ontogeny with series of adults—real phylogeny. This method of work is difficult to pursue with living forms, and still more so with fossils, although much that is good and reliable has been done with both.

The fossils that best lend themselves for this sort of work are the *Ammonoidea*, a group of cephalopods that lived from the beginning of the Devonian to the end of the Cretaceous. Being wholly extinct, the group is classified entirely by external markings, such as are capable of being preserved in



fossils. Such marks are the sutures, the shape of the whorl, and surface ornamentation. Then, too, the ammonoids in growth envelop and protect the chambers of the earlier stages, thus preserving in a single individual a complete record of their larval history. By pulling off these outer coils the naturalist can obtain the shell in any desired stage, and can prevent the possibility of mistakes by selecting adults to start with. A study of the ontogeny of a fossil ammonoid may thus be carried on with as great accuracy as if the naturalist could hatch out and bring up the young animal in a marine laboratory.

Many authors have worked on the phylogeny of Mesozoic ammonites, and Hyatt has used especially the comparison of stages of growth of the individual with successive genera and species. But Mesozoic forms are so far from their origin that their ontogeny is long and the meaning of larval stages obscure. If we wish to learn the history of the race we must go back to the ammonoids of the Paleozoic, the goniatites. These forms, being nearer their origin, have shorter larval periods and go through fewer stages of growth; their interpretation is therefore simpler. Branco accumulated a considerable mass of exact data on the ontogeny of several goniatites, but without correlating these stages with genera. His figures are just as good and reliable as if he had done so; but since he was not looking for certain stages of growth, often the very ones we should like most to see have not been figured, due no doubt to lack of specimens. Karpinsky, in the same way, has worked out the ontogeny of *Pronorites* and *Medlicottia*, and the phylogeny of the *Prolecanitidae*. Outside of this work the ontogeny of the goniatites is unknown, and they have been grouped together arbitrarily, often in contradiction to their true relationships. Probably so little work has been done in this line because of scarcity of specimens, especially such as can be taken apart to expose the larval stages. Paleozoic rocks have nearly everywhere been subjected to alteration and deformation, so that while species can be described from material found in them, it is rarely that one finds the inner whorls well preserved in cephalopods.



It was known to Quenstedt and L. von Buch that ammonites went through a goniatite stage in their youth; but these earlier paleontologists did not realize the importance and value of this fact, since they did not connect the idea with evolution, and hence they did not use their knowledge as a guide in classification. But we now know that the only way ever to work out the phylogeny of the ammonites is to study the development of the goniatites.

#### CLASSIFICATION OF GONIATITES.

Beyrich<sup>1</sup> first recognized the unwieldiness of the old genus *Goniatites* and attempted to subdivide it as follows:

1. *Nautilini* (*Anarcestes* and *Mimoceras*). 2. *Simplices* (*Tornoceras*, *Brancoceras*, and *Prionoceras*). 3. *Aequales* (*Sporadoceras* and *Prolecanites*). 4. *Irregulares* (*Beloceras*). 5. *Primordiales* (*Gephyroceras*). 6. *Carbonarii* (*Glyphioceratidæ* p. p. *Glyphioceras* and *Gastrioceras*).

This classification still holds sway, except in text-books of paleontology; for the genera and families into which later writers have divided the goniatites have not generally been accepted by paleontologists.

Afterward another classification was attempted by G. and F. Sandberger,<sup>2</sup> which agreed substantially with that of Beyrich, except in the names given to the groups. Neither the divisions of Beyrich nor of Sandberger were intended to represent genera or families, for they mostly contain heterogeneous elements; and even at that time the old genus *Ammonites*, comprising several times as many species as the goniatites, and very much more various in form, was still considered a unit.

The first attempt to distinguish genera among the goniatites was made by Dr. E. von Mojsisovics<sup>3</sup> in 1882, who named *Anarcestes*, *Aphyllites*, *Pinacites*, *Pronorites*, *Prolecanites*, and *Pericyclus*, and brought them into rather fan-

<sup>1</sup> Beitr. Kennt. Verstein. Rhein. Uebergangsgebirge. Abhandl. Berlin Akad. Wiss., 1837.

<sup>2</sup> Verstein. Rhein. Schichtensystems in Nassau.

<sup>3</sup> Cephalopoden d. Mediterranen Trias-Provinz.



ciful relationships to his genera of Triassic ammonites. The only systematic attempt to group all goniatites into genera and families is Hyatt's classification, "Genera of Fossil Cephalopods,"<sup>1</sup> where all known species were grouped into genera, and these in turn in five families: *Nautilinidæ*, Lower and Middle Devonian; *Primordialidæ*, Upper Devonian; *Magnosellaridæ*, Middle and Upper Devonian; *Glyphioceratidæ*, Upper Devonian, Carboniferous, and Permian; *Prolecanitidæ*, Upper Devonian, Carboniferous, Permian, and Trias.

Steinmann<sup>2</sup> groups the goniatites into two families supposed to be derived from the two chief genera of the *Nautilinidæ*, *Anarcestes*, and *Mimoceras*. On page 399 of his work is given a table showing the supposed genetic connection of the various genera and also their relationship to their ammonite successors of the Mesozoic. These relationships, however, are purely speculative, and not based on ontogenetic study of the groups.

Zittel in his later work<sup>3</sup> recognizes only two families, *Goniatitidæ* and *Prolecanitidæ*, of which the former comprises the *Nautilinidæ*, *Primordialidæ*, *Magnosellaridæ*, and *Glyphioceratidæ*. These subdivisions may then be retained with the rank of subfamilies.

#### GLYPHIOCERATIDÆ Hyatt.

This group was established by Hyatt<sup>4</sup> to include a number of species from the Upper Devonian, Carboniferous, and Permian. The oldest genera are *Brancoceras* and *Prionoceras*, which began in the Upper Devonian, attained their acme in the Lower Carboniferous, and lived on into the Coal Measures. Both genera are smooth-shelled, and both have a pointed, undivided, ventral lobe, and two pairs of lateral lobes, of which the first is angular; the saddles of most species of both genera are broadly rounded,

<sup>1</sup> Proc. Boston Soc. Nat. Hist., 1883, Vol. XXII.

<sup>2</sup> Elemente der Palæontologie, 1890.

<sup>3</sup> Grundzuege der Palæontologie, 1895.

<sup>4</sup> Proc. Boston Soc. Nat. Hist., Vol. XXII, p. 322.



although on the type of *Prionoceras*, *Goniatites belvalianus* de Koninck, the first lateral saddles are angular. The only difference between the two genera is that *Brancoceras* is compressed, high-whorled, almost discoidal, and very involute; while *Prionoceras* is broad, low-whorled, and evolute. Hyatt considers *Brancoceras* as the radicle of the *Glyphioceratidæ*, and traces the group from *Anarcestes* of the Lower Devonian, through *Tornoceras* (*Parodiceras*) of the Middle Devonian. He admits the near relationship between the two genera, but considers *Prionoceras* as the link between the supposed radicle *Brancoceras* and *Glyphioceras*. The genealogy of the *Glyphioceratidæ*, according to Hyatt, is as follows:

|                                   |                                                                                                 |
|-----------------------------------|-------------------------------------------------------------------------------------------------|
| Anarcestes→Tornoceras→Brancoceras | {Prionoceras→Glyphioceras<br>Münsteroceras→Gastrioceras→Paralegoceras<br>Dimeroceras→Pericyclus |
|                                   |                                                                                                 |
|                                   |                                                                                                 |

Professor K. A. von Zittel<sup>1</sup> has recently merged *Prionoceras* in *Brancoceras*, not even giving subgeneric rank to the former. But even though they may be nearly related, their phylogeny justifies the separation. Both genera undoubtedly branched off about the same time from *Tornoceras* in the Upper Devonian, but *Brancoceras* is not the radicle. While it is possible, although not known, that *Münsteroceras* may go through a *Brancoceras* stage, *Prionoceras* does not, neither does *Glyphioceras*. *Prionoceras* comes directly from *Tornoceras*, and in turn gives rise to *Glyphioceras*. It seems likely, too, that some species of *Gastrioceras* descended directly from *Prionoceras* by division of the ventral lobe, while others may have come from *Münsteroceras*. In any case, whether it came off from the radicle, or through *Münsteroceras*, *Gastrioceras* is a later branch than *Glyphioceras*, not being certainly known below the Coal Measures, and having its maximum in the Upper Coal Measures; it therefore deserves to rank as an independent genus. It also seems proper to retain *Prionoceras* and *Brancoceras* with full generic rank, and *Münsteroceras* as subgenus under *Glyphioceras*.

<sup>1</sup> Grundzuge der Palaeontologie, 1895, p. 398.



Genus *Glyphioceras* Hyatt.

This genus was established by Hyatt<sup>1</sup> to include Carboniferous species with semilunular whorls, usually broad and rather low; with divided ventral lobe, and a pair of angular lateral lobes; with the shell usually smooth, but in some cases with weak umbilical ribs; with periodic constrictions or varices. *Goniatites crenistria* Phillips (considered by many paleontologists as a synonym of *G. sphaericus* Martin, the type of the race of goniatites), was chosen as type of the genus. *Glyphioceras* was divided into two groups: The first with narrow umbilici, and no umbilical ribs at all, or only very weak ones; to this division belong *G. sphaericum* Martin, *G. crenistria* Phillips, and many others. The second group contains species with wider umbilici, and often with strong umbilical ribs; to this group belong *G. diadema* Goldfuss, and several others. Zittel<sup>2</sup> emended the genus, and included in it *Münsteroceras*, *Nomismoceras*, and *Homoceras*. Karpinsky<sup>3</sup> afterward attempted to show that *Glyphioceras* and *Gastrioceras* grade over into each other, and that there is no reason for retaining the two as independent genera. But just this same thing might be said of any two nearly related genera. There is certainly no difficulty in distinguishing typical members of both groups; and since *Gastrioceras* is a later branch than *Glyphioceras*, it facilitates phylogenetic study to consider them as distinct. As thus emended and restricted, *Glyphioceras* contains species from the Carboniferous, ranging from the Waverly horizon, goniatite-beds of Rockford, Indiana, the very base of the system, up into the Permian.

Little work has been done on the phylogeny of this genus, notwithstanding its importance as the chief member of the Carboniferous ammonoids and the type of the whole race of goniatites. The first observations were made by Hyatt<sup>4</sup>,

<sup>1</sup>Proc. Boston Soc. Nat. Hist., Vol. XXII, p. 328.

<sup>2</sup>Handbuch der Paläontologie, Abtheil I, Band II, p. 420.

<sup>3</sup>Mém. Acad. Sci. St. Petersburg, Tome XXXVII, No. 2. Ammonéen der Artinsk-Stufe, p. 46.

<sup>4</sup>Bull. Mus. Compar. Zoöl., Vol. III, 1872, No. 5, Pl. II, figs. 3 and 4.



who figured a larva of *Glyphioceras diadema* Goldfuss, consisting of the protoconch with two-thirds of the first whorl attached. Branco<sup>1</sup> afterward figured the protoconch and two larval stages of *G. diadema* at diameters of 0.66 mm., and 0.90 mm. respectively. He noted, too, that on this species the ventral lobe became divided at a diameter of six millimetres, although his figure I, on Plate IV, shows the ventral lobe broadening and preparing for division at diameter of 2.25 mm. But the consecutive larval stages were not figured and described, nor were they compared with known genera, although that does not lessen the value of his data.

Hyatt in his "Genera of Fossil Cephalopods" often compares the larvæ of this group of goniatites to their ancestral genera, but as the paper is not accompanied by illustrations and systematic descriptions of stages of growth of the species cited, it is not easy to follow the correlations. It was therefore desirable that some typical species of *Glyphioceras* should be studied in detail from the protoconch upwards, and material suitable for this was found in *G. incisum* Hyatt, from the Fayetteville shale, Warsaw division of the Lower Carboniferous, at Moorefield, Independence County, Arkansas.

*Glyphioceras incisum* Hyatt.

PLATES XIII-XV.

*Glyphioceras incisum* Hyatt, Geol. Surv. Texas, Fourth An. Report, p. 471, Pl. XLVII, figs. 44-48.

The form is globose, broad, low-whorled, with semilunar cross-section, and very involute; in the adult the umbilicus is closed so that the inner whorls are concealed. The abdomen is broadly rounded and slightly flattened, while the umbilical shoulders slope steeply inwardly. There are four or five constrictions to a whorl, visible both on the shell and on the cast. These occurred even in the early larval stages, beginning at a diameter of 0.90 mm., and lasting until old age.

<sup>1</sup> Palæontographica, Vol. XXVII. Beiträge z. Entwick. Foss. Ceph., Pl. IV, fig. 1.



The shell is marked with distinct cross striæ of growth, with fine sharp crenulations, which show only toward maturity. The elevations between the pits of the crenulations become in the adult indistinct spiral ridges, giving a finely reticulated aspect to the surface. The cross striæ and spiral ridges are not visible on the cast. In the adult stage the surface is ornamented with undulating growth bands, forming weak ribs strongest near the umbilicus and distinctly visible on the cast. These originate from bundling of the cross striæ at the umbilicus, and give the shell a decided resemblance to the Triassic genus *Fuvavites*, which may very possibly be a descendant of *Glyphioceras*. This bundling begins at about 2.3 mm. diameter.

The visible sutures consist of a pair of pointed ventral lobes (divided by a notched saddle) and a pair of angular lateral lobes. All the lobes and the first pair of lateral saddles are angular in the adult, while the second pair of saddles is broadly rounded. A second pair of lateral lobes is on the umbilical shoulders, just concealed by the involution. The internal sutures consist of a pointed antisiphonal or dorsal lobe, and a pair of similar lateral lobes. In the early part of the adult stage the lateral saddles are rounded, as shown on Pl. XV, fig. 11, on a specimen of 15 mm. diameter. In the youthful stages all the saddles are broad and the lobes only slightly pointed.

#### MEASUREMENT OF SPECIMENS OF ADULT AGE.

|                                          | mm.   | mm.   | mm.   | mm.   |
|------------------------------------------|-------|-------|-------|-------|
| Diameter .....                           | 15.00 | 20.7  | 23.00 | 31.5  |
| Height of last whorl .....               | 7.25  | 8.2   | 12.5  | 17.0  |
| Height of last whorl from the preceding. | 4.00  | 4.0   | ..... | ..... |
| Width of last whorl .....                | 12.00 | 15.7  | 20.5  | 24.5  |
| Involution. ....                         | 3.25  | 4.2   | 7.5   | ..... |
| Width of umbilicus .....                 | 1.70  | ..... | ..... | ..... |



*Position and Locality.*—*Glyphioceras incisum* was found in the Fayetteville shale, Warsaw division of the Lower Carboniferous, at Moorefield, Independence County, Arkansas, accompanied by *Nautilus (Endolobus) spectabilis* Meek, *Productus semireticulatus* Martin, *P. cora* d'Orbigny, *Spirifer lineatus* Martin, *S. glaber* Martin, *Terebratula bovidens* Meek, and numerous other less characteristic species. The specimens of *G. incisum* from the Moorefield beds agree exactly with those described by Hyatt from the Bend formation, Carboniferous, five miles west of Lampasas, Texas. In the same paper Hyatt<sup>1</sup> describes *Glyphioceras cumminsi*, also from the Bend formation; he compares *G. cumminsi* to *G. striatum* Sowerby and *G. crenistria* Phillips, finding, however, points of difference from both. European paleontologists now regard *G. striatum* and *G. crenistria* as synonymous, and many go so far as to place both as synonyms under *G. sphaericum* Martin. To this last species Hyatt compares *G. incisum*, but finds that *G. incisum* lacks the crenulations which *G. sphaericum* has, and agrees with it in lacking spiral ridges. *G. incisum* is certainly very nearly related to *G. sphaericum*, and if the European forms *G. crenistria* and *G. striatum* are all identical with *G. sphaericum*, the American form might also very well be classed as a variety under that species, especially as *G. incisum* as an adult has distinct crenulations. The European Carboniferous faunas are turning out to be much more closely related to those of the Mississippi Valley than has been recognized heretofore. In a recent paper the writer<sup>2</sup> has described from the Coal Measures of Arkansas the following European Coal Measure forms not before known in America: *Conocardium aliforme* Sowerby, *Gastrioceras marianum* Verneuil, *Pronorites cyclolobus* Phillips, besides many others known before in America. Thus the presumption is not against the identity of very similar forms in the two regions, but rather in favor of it.

<sup>1</sup> Op. cit., p. 467, Pl. XLVII, figs. 33-43.

<sup>2</sup> Proc. Am. Phil. Soc., Vol. XXXV, 1896, No. 152, "Marine Fossils from the Coal Measures of Arkansas."



## LARVAL STAGES.

In order to obtain the larval stages of *Glyphioceras incisum*, a number of adults were selected, so as to make sure of the identity, and the outer coils were broken off until the desired size was obtained. This necessitated the destruction of several specimens, but was well worth while in view of reliability of the results. The specimens were studied in three different mountings, dry on card-board, in a drop of water on card-board, and in water in a watch-glass over a strong condensing lens. In the first way the surface markings are seen best, in the second the sutures and form, in the third the internal structure when the specimen is translucent. The nomenclature used is that of Hyatt, published in "Phylogeny of an Acquired Characteristic."<sup>1</sup>

*Phylembryonic.* The protoconch represents the first shell secreted by the shell-gland, and must have been formed while the animal was in the egg. It is quite possible that some of the chambers were formed before the egg was hatched, but this cannot be determined on fossils. The protoconch is taken for convenience to represent the phylembryonic stage of growth, the end of the embryonic, when the class or phylum can be determined, and the animal is already a cephalopod. In shape, the protoconch is a smooth, rather elongate, bobbin-shaped, oval body, of which the upper part projects forward in a lap, where the first chamber was joined to it. The protoconch was not the whole of the embryo chamber, for a part of the spiral tube must have furnished a lodging for the embryo; but after the formation of the first air-chamber it is no longer possible to determine how long the primitive body-chamber was. The protoconch corresponds to the primitive nautilian shell from which the ammonoids descended, but the parallelism is not exact, for the initial chamber of the nautiloids is not calcareous, while acceleration of development has pushed back to the embryo the calcareous shell of the ammonoids.

In the protoconch is seen the beginning of the siphon, or

---

<sup>1</sup>Proc. Am. Phil. Soc., Vol. XXXII, No. 143.



siphonal *cæcum*, a pear-shaped knob, projecting a short distance into the embryonic shell. It must have been present in the embryo, for it is older than the first suture, but its function is unknown. In some specimens what seemed to be a tube could be seen attached to the *cæcum*; this is probably the prosiphon described by Munier-Chalmas, but no specimens sufficiently definite to figure could be obtained.

On Pl. XIII, figs. 1 and 2, is shown the protoconch from which all the chambers have been broken off. Dimensions:

|                                                     | mm.  |
|-----------------------------------------------------|------|
| Diameter.....                                       | 0.46 |
| Height of whorl at attachment of first chamber..... | 0.24 |
| Height of first chamber from protoconch.....        | 0.17 |
| Width.....                                          | 0.66 |
| Involution.....                                     | 0.07 |

The protoconch is constant in size and dimensions, for several specimens were obtained free from the air-chambers. Also a number of others were broken back almost to the protoconch, and the dimensions agreed, as nearly as could be determined.

On Pl. XIII, figs. 3, 4, and 5, is shown the protoconch of a *Glyphioceras* from the Carboniferous of Scott County, Arkansas, 2 N., 29 W., section 36, near the center. This species was compared by the writer<sup>1</sup> to *G. sphaericum* Martin, and said to be identical with the species from Moorefield. But although the adults are nearly alike, the protoconchs are quite unlike, as may be seen by a comparison of the two figures. The following are the dimensions of the Scott County form:

|                                                      | mm.  |
|------------------------------------------------------|------|
| Diameter.....                                        | 0.53 |
| Height of whorl at attachment to the protoconch..... | 0.26 |
| Height of whorl from the protoconch.....             | 0.18 |
| Width.....                                           | 0.80 |
| Involution.....                                      | 0.08 |

These figures show it to be larger and proportionally broader than the typical *G. incisum*. If the species are identical then this is an unusual variation.

<sup>1</sup> "Marine Fossils from the Coal Measures of Arkansas," p. 11.



*Ananepionic.* As soon as the first air-chamber is formed the animal has left the embryonic and begun the larval stage, and then takes rank with the chambered nautiloids. The suture at this stage consists of a very broad ventral saddle with a pair of narrow lateral lobes. On Pl. XIII, fig. 1, is shown this suture; fig. 6 shows this and also the second chamber-wall; figs. 9 and 10 show the ananepionic suture with half a coil attached. Pl. XV, fig. 1, shows the initial suture along with the later ones. While this stage cannot be compared to any particular genus, it corresponds to some nautilian form of the Silurian. The ananepionic siphon is about half-way between the dorsum and the venter, in this character, too, agreeing with the nautiloids. Where the siphon passes through the partition the wall is bent backward in a cone and has a siphonal collar around the tube. The surface is still smooth, no ornamentation of any sort ever having been seen on early stages of ammonoids.

*Metanepionic.* With the second larval substage the shell becomes a true ammonoid; this begins with the second suture, which takes on the ventral lobe of the goniatites. The shell is smooth as before, and the whorl changes little in shape, being still low, broad, and little embracing. The sutures and shape correspond exactly to *Anarcestes*, the primitive goniatite and radicle of the ammonoids. *Anarcestes* was named but not characterized by Mojsisovics,<sup>1</sup> and afterward defined by Hyatt<sup>2</sup> as containing forms with smooth, broad, and low whorls, with semilunular cross-section, deep umbilicus, and rather broad abdomen. *Goniatites subnautilus* Schlotheim, of the Middle Devonian, was chosen as type of the genus, but most of the species occur in the Lower Devonian, in the Hercynian beds, which were formerly assigned to the Upper Silurian.

*Glyphioceras incisum* shows the *Anarcestes* stage at the second and third sutures, and resembles closely *A. lateseptatus* Beyrich of the Lower Devonian. On Pl. XIII, fig. 6, is seen the transition from the ana- to the metanepionic;

<sup>1</sup>"Cephalopoden der Mediterranen Trias-Provinz," p. 181.

<sup>2</sup>"Genera of Fossil Cephalopods," p. 309.



figs. 9 and 10 show the transition from ananepionic (first suture) to metanepionic (second and third sutures); figs. 11 and 12 show the *Anarcestes* stage at the first and second sutures visible on the whorl. The metanepionic sutures, seen in projection on Pl. XV, figs. 2 and 3, consist of a deep, rounded, ventral lobe, and a pair of broad, shallow, lateral lobes. When the animal has progressed thus far in its development it is a true goniatite, and the siphon has already turned to the outside of the whorl, or abdomen. On Pl. XV, fig. 12, are shown for comparison the sutures of *A. subnautilus* (after L. von Buch, *Gesammelte Werke*, Vol. IV, p. 116, Pl. XI, fig. 9).

*Paranepionic.* When the broad lateral lobes become indented with a pair of lateral saddles, the sutures, the narrow umbilicus, and the broad, low whorl all correspond to *Tornoceras* Hyatt, of the Middle and Upper Devonian. *G. incisum* reaches this stage at the fourth suture, at a diameter of about 0.68 mm., one-third of a whorl, and continues in it for the fourth, fifth, and sixth sutures, up to a diameter of 0.80 mm., and five-eighths of a whorl. Pl. XIII, figs. 9 and 10, shows the form at the *Tornoceras* stage, at one-half a whorl, with the following dimensions:

|                                           | mm.  |
|-------------------------------------------|------|
| Diameter.....                             | 0.74 |
| Height last coil.....                     | 0.38 |
| Height last coil from the protoconch..... | 0.13 |
| Width of last whorl .....                 | 0.77 |
| Involution.....                           | 0.26 |
| Width of umbilicus.....                   | 0.06 |

On Pl. XIII, figs. 11 and 12, the *Tornoceras* stage shows at the fourth, fifth, and sixth sutures.

*Neanic.* When the ammonoid in its growth no longer shows the characters of its distant ancestors, but has already taken on those of its own family, it may be said to have left the larval stage proper and to have begun its youth. The ananeanic is then the beginning of the adolescent period. *G. incisum* at the seventh suture, three-fourths of a whorl, and diameter of 0.85 mm., changes its form markedly; the two pairs of lateral lobes become more pronounced, and



the ventral lobe becomes smaller in proportion; the coil leaves its close spiral and shows decided egression, the umbilicus becomes wider, while the chamber becomes actually narrower than in the *Tornoceras* stage, as seen from these figures: width of chamber at diameter 0.74 mm. is 0.77 mm., at diameter 0.92 mm. it is 0.69 mm. The involution also becomes less. At diameter 0.90 mm. and end of the first whorl a decided constriction, marking a temporary mouth of the shell, makes its appearance. This stage corresponds to the Upper Devonian and Carboniferous genus *Prionoceras* Hyatt,<sup>1</sup> of which *P. divisum* Muenster, of the Upper Devonian, and *P. belvalianum* de Koninck, of the Lower Carboniferous, are the types. These species have broad, low, rather evolute whorls, with wide umbilici and smooth surfaces, ornamented only with periodic constrictions. The external sutures consist of an undivided, pointed, ventral lobe, one pair of angular lateral lobes, and a second pair of rounded lobes on the umbilical border. The external saddles are angular and the lateral saddles rounded and broad. To this genus may also be assigned *Goniatites compactus* Meek and Worthen, Geol. Survey Illinois, Vol. V, p. 611, Pl. XXXI, fig. 2, of the Coal Measures; and *G. greencastlensis* Miller and Gurley, Bull. XI, Illinois State Mus. Nat. Hist., p. 44, Pl. V, figs. 12-14, from the St. Louis group of the Lower Carboniferous. These species differ from the types in the rounded external saddles, but in this respect they agree with the ananeanic substage of *G. incisum*. The beginning of the *Prionoceras* stage is shown on Pl. XIII, figs. 11 and 12, in the widening of the umbilicus, egression of the spiral, and narrowing of the chamber. Dimensions of the specimen:

|                                              | mm.  |
|----------------------------------------------|------|
| Diameter .....                               | 0.92 |
| Height of last whorl .....                   | 0.33 |
| Height of last whorl from the preceding..... | 0.23 |
| Width of last whorl.....                     | 0.69 |
| Involution .....                             | 0.10 |
| Width of umbilicus .....                     | 0.30 |

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<sup>1</sup> "Genera of Fossil Cephalopods," p. 328.



This stage begins at 0.85 mm. diameter, three-fourths of a whorl from the protoconch, and lasts with little change except increase in size for two revolutions up to a diameter of 2.25 mm., when the transition to *Glyphioceras* begins.

Plate XIV, figs. 1 and 2, shows a continuation of the *Prionoceras* stage, at one and three-fourths whorls, with dimensions:

|                                              | mm.  |
|----------------------------------------------|------|
| Diameter .....                               | 1.29 |
| Height of last coil .....                    | 0.45 |
| Height of last coil from the preceding ..... | 0.29 |
| Width of last coil .....                     | 0.95 |
| Involution .....                             | 0.15 |
| Width of umbilicus .....                     | 0.50 |

On this specimen are seen two constrictions about two-thirds of a revolution apart, thus making the resemblance to *Prionoceras* very striking. At this stage are first seen the cross striæ of growth. A continuation of the same generic stage is shown on Pl. XIV, figs. 3 and 4, at one and seven-eighths whorls, and dimensions:

|                                               | mm.  |
|-----------------------------------------------|------|
| Diameter .....                                | 1.38 |
| Height of last coil .....                     | 0.52 |
| Height of last whorl from the preceding ..... | 0.31 |
| Width of last whorl .....                     | 1.02 |
| Involution .....                              | 0.21 |
| Width of umbilicus .....                      | 0.51 |

The relative dimensions are nearly the same as at diameters 0.92 mm. and 1.29 mm., but the sutures differ slightly, the ventral lobe being slightly blunted, as shown on Pl. XV, fig. 8. On this specimen only one constriction was visible at diameter of 0.85 mm.

On Pl. XIV, figs. 5 and 6 show a larger specimen still in the *Prionoceras* stage, at two and one-eighth whorls. Dimensions:

|                                               | mm.  |
|-----------------------------------------------|------|
| Diameter .....                                | 1.64 |
| Height of last whorl .....                    | 0.60 |
| Height of last whorl from the preceding ..... | 0.40 |
| Width of last whorl .....                     | 1.38 |
| Involution .....                              | 0.20 |
| Width of umbilicus .....                      | 0.54 |



No constrictions were visible on this specimen; that one which occurs at end of the first whorl being concealed by the outer coil. The relative dimensions are nearly the same as on the preceding specimens, except that the last whorl is proportionally broader and the umbilicus narrower. The sutures are the same as on the last specimen. The end of the *Prionoceras* stage is shown on Pl. XIV, figs. 7 and 8, at two and three-fourths of a whorl. Dimensions:

|                                               | mm.  |
|-----------------------------------------------|------|
| Diameter .....                                | 2.25 |
| Height of last whorl .....                    | 0.87 |
| Height of last whorl from the preceding ..... | 0.50 |
| Width of last whorl .....                     | 1.82 |
| Involution .....                              | 0.37 |
| Width of umbilicus .....                      | 0.58 |

No constrictions were visible on this specimen, the earlier ones being concealed by the outer whorl. The figures show that the relative dimensions remain nearly as before, but the umbilicus becomes considerably narrower. The sutures are like those of the smaller specimens, but on the last half-whorl the ventral lobe becomes very much flattened, and at diameter of 2.2 mm. becomes slightly indented by the beginning of a ventral saddle, thus showing a transition to *Glyphioceras*, and the end of the adolescent stage. No youthful stages larger than this were successfully broken out in condition to figure, but the imperfect ones obtained showed a gradual narrowing of the umbilicus and increase in height of the whorl and involution.

#### ADULT STAGE.

The form of the adult *Glyphioceras incisum* has already been sufficiently described in this paper and in Hyatt's monograph. The sutures changed in increasing depth of the ventral sinus and sharpening of the lateral lobes, as shown on Pl. XV, fig. 11, taken from a specimen of diameter of 15 mm. The early adult sutures have been figured by Hyatt, Geol. Survey Texas, Fourth An. Rep., Pl. XLVII, figs. 44-45.



Plate XIV, fig. 9, shows the smallest specimen obtained of the adult stage; it agrees in all essentials with those of larger growth, only the ventral saddle is shorter and the lateral saddles more rounded.

TABLE OF STAGES OF GROWTH.

|                                                   | Proto-<br>conch. | Proto-<br>conch and<br>two<br>chambers. | One-half<br>whorl,<br><i>Anarcestes</i><br>to<br><i>Tornoceras</i> | First<br>whorl,<br><i>Tornoceras</i><br>to<br><i>Priono-<br/>ceras</i> . | <i>Priono-<br/>ceras</i><br>stage<br>1½ whorls | <i>Priono-<br/>ceras</i><br>1¾ whorls. | <i>Priono-<br/>ceras</i><br>2¾ whorls. | <i>Priono-<br/>ceras</i><br>2¾ whorls. |
|---------------------------------------------------|------------------|-----------------------------------------|--------------------------------------------------------------------|--------------------------------------------------------------------------|------------------------------------------------|----------------------------------------|----------------------------------------|----------------------------------------|
|                                                   | mm.              | mm.                                     | mm.                                                                | mm.                                                                      | mm.                                            | mm.                                    | mm.                                    | mm.                                    |
| Diameter.....                                     | 0.46=1.00        | 0.61=1.00                               | 0.74=1.00                                                          | 0.92=1.00                                                                | 1.29=1.00                                      | 1.38=1.00                              | 1.64=1.00                              | 2.25=1.00                              |
| Height of last<br>whorl.....                      | 0.24=0.52        | 0.31=0.50                               | 0.38=0.52                                                          | 0.33=0.35                                                                | 0.45=0.34                                      | 0.52=0.38                              | 0.60=0.36                              | 0.87=0.38                              |
| Height of last<br>whorl from the<br>preceding.... | 0.17=0.36        | 0.15=0.24                               | 0.13=0.17                                                          | 0.23=0.25                                                                | 0.29=0.22                                      | 0.31=0.22                              | 0.40=0.23                              | 0.50=0.22                              |
| Width of last<br>whorl.....                       | 0.66=1.56        | 0.66=1.08                               | 0.77=1.04                                                          | 0.69=0.75                                                                | 0.95=0.73                                      | 1.02=0.73                              | 1.38=0.84                              | 1.82=0.80                              |
| Involution.....                                   | 0.07=0.15        | 0.16=0.26                               | 0.26=0.35                                                          | 0.10=0.10                                                                | 0.15=0.11                                      | 0.21=0.15                              | 0.20=0.12                              | 0.37=0.16                              |
| Width of umbil-<br>icus.....                      |                  |                                         | 0.06=0.08                                                          | 0.28=0.30                                                                | 0.50=0.38                                      | 0.51=0.37                              | 0.54=0.32                              | 0.58=0.25                              |

|                                           | <i>Prionoceras</i><br>to<br><i>Glyphioceras</i> . | <i>Prionoceras</i><br>to<br><i>Glyphioceras</i> .<br>End of<br>neanic. | <i>Glyphioceras</i> .<br>Anephebic. | <i>Glyphioceras</i> |
|-------------------------------------------|---------------------------------------------------|------------------------------------------------------------------------|-------------------------------------|---------------------|
|                                           | mm.                                               | mm.                                                                    | mm.                                 | mm.                 |
| Diameter.....                             | 2.60=1.00                                         | 3.00=1.00                                                              | 6.00=1.00                           | 11.00=1.00          |
| Height of last whorl.....                 | 1.24=0.47                                         | 1.45=0.48                                                              | 3.50=0.58                           | 5.50=0.50           |
| Height of last whorl from the preceding.. | 0.76=0.29                                         | 0.83=0.27                                                              | 1.80=0.30                           | 3.00=0.27           |
| Width of last whorl.....                  | 2.32=0.88                                         | 2.82=0.94                                                              | 6.00=1.00                           | 10.00=0.90          |
| Involution.....                           | 0.48=0.18                                         | 0.62=0.20                                                              | 1.65=0.27                           | 2.50=0.22           |
| Width of umbilicus.....                   | 0.61=0.23                                         | 0.66=0.22                                                              | 0.90=0.15                           | 1.00=0.09           |

## SUMMARY OF RESULTS.

The ontogeny of *Glyphioceras* is of interest not only for its own sake, but also because it is the most important genus of the largest family of ammonoids of the Carboniferous, and because this family gave rise to a large part of the am-



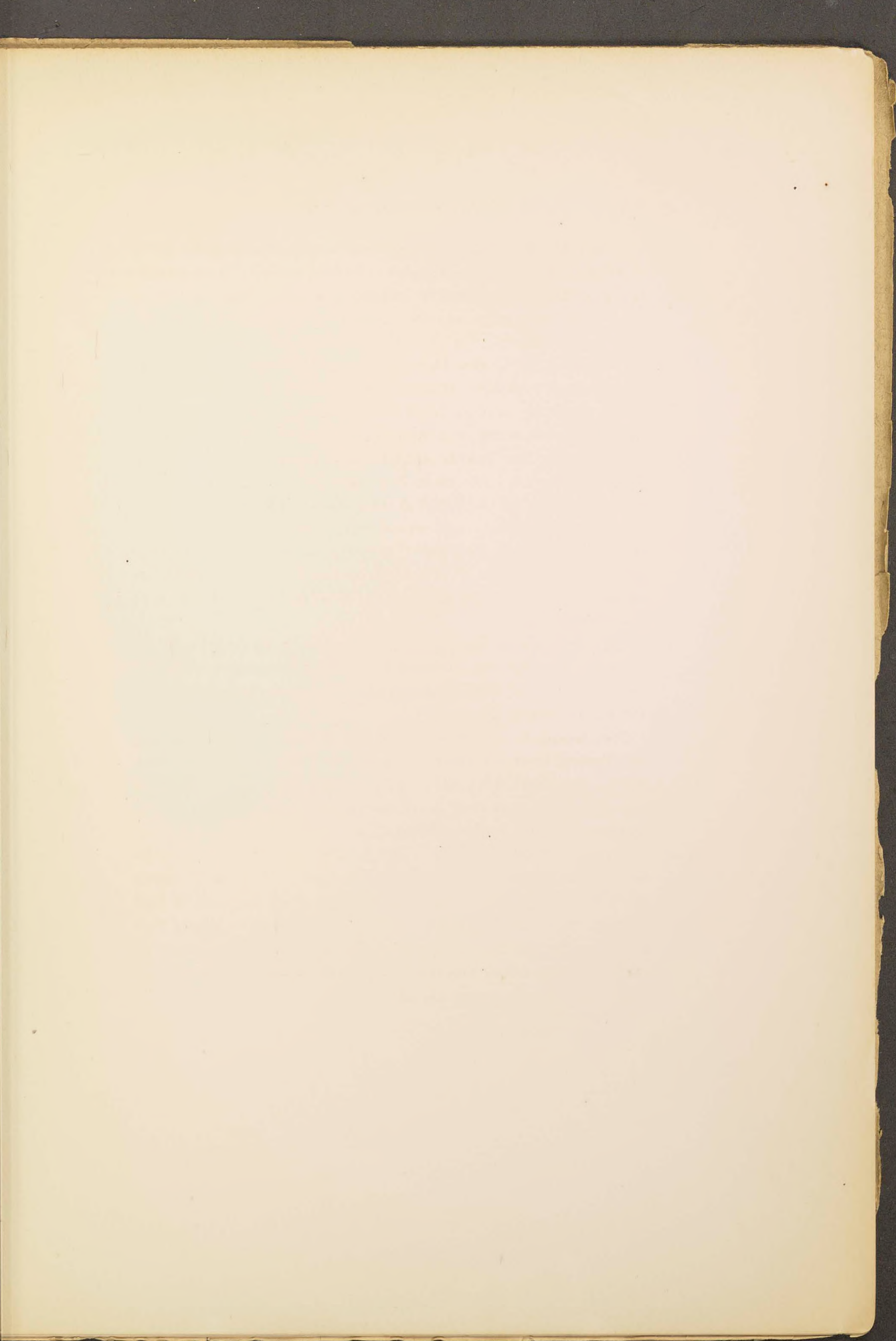
monites of the Trias. *Glyphioceras* in its ontogeny goes through the following stages: phylembryonic, protoconch, representing the primitive cephalopod; ananepionic, Silurian nautiloid; metanepionic, *Anarcestes* of Lower Devonian; paranepionic, *Tornoceras* of Middle Devonian; neanic, *Prionoceras* of Upper Devonian and Carboniferous, showing gradual transition through ana-, meta-, and paraneanic, and a gradual change from *Prionoceras* to *Glyphioceras* in the late adolescent and early adult stages. *Prionoceras* is undoubtedly the family radicle, and *Brancoceras* is a side-branch, since *Glyphioceras* does not go through any stage corresponding to the latter genus. *Gastrioceras* comes from *Prionoceras* (through *Münsteroceras*) by somewhat narrowing the whorl and division of the ventral lobe. *Glyphioceras* comes directly from *Prionoceras* by narrowing the umbilicus so as to conceal most of the inner whorls and by division of the ventral lobe.

The division of the subfamily *Glyphioceratidæ* into *Brancoceras*, *Prionoceras*, *Pericyclus*, *Glyphioceras*, (subgenus *Münsteroceras*), *Gastrioceras*, *Paralegoceras*, is quite proper for phylogenetic reasons.

According to Steinmann the *Ceratitidæ* of the Trias are descended from *Gastrioceras*, and the *Tropitidæ* from *Pericyclus*, but neither of these groups goes through stages of growth corresponding to these genera. *Tropites* does, however, go through a *Prionoceras* stage, and later it resembles closely *Gastrioceras*, but it already has the *Tropites* keel before the ventral lobe is divided. It then descends from the *Glyphioceratidæ*, but directly from the radicle and not through any modified form. But it is quite likely that some of the genera assigned to the *Tropitidæ* do descend directly from other members of the *Glyphioceratidæ*.

LELAND STANFORD JUNIOR UNIVERSITY,  
CALIFORNIA,  
October, 1897.







## EXPLANATION OF THE FIGURES.

## PLATE XIII.

All figures on this plate are forty times enlarged.

*Glyphioceras incisum* HYATT.

Figs. 1, 2. Protoconch. 1, from above; 2, from front. Diameter 0.46 mm.

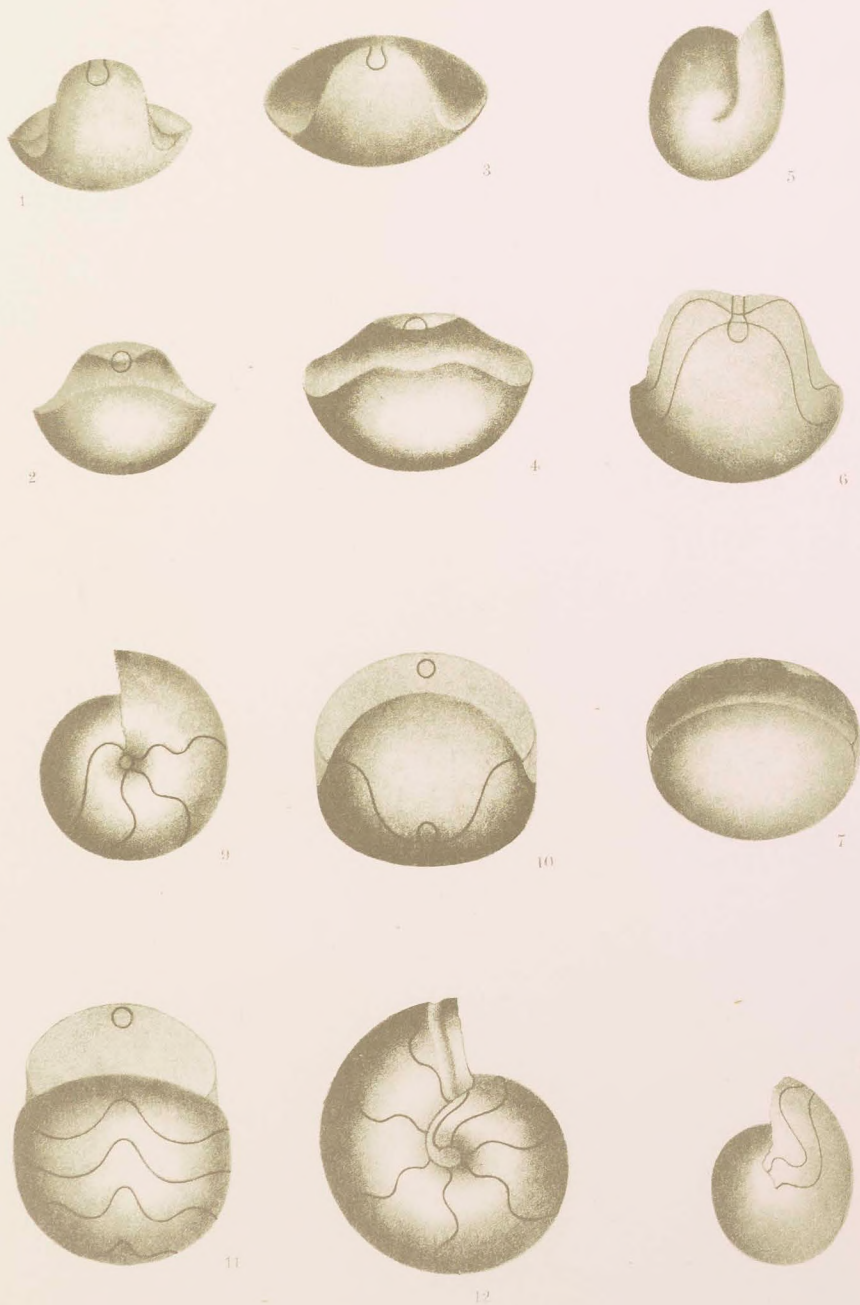
Figs. 3, 4, 5. Protoconch of same or a nearly related species from Scott County, Arkansas. 3, from above; 4, from front; 5, from side.

Figs. 6, 7, 8. Protoconch with first two sutures. 6, from above; 7, from front; 8, from side.

Figs. 9, 10. Larval stage, diameter of 0.74 mm., protoconch and one-half of first whorl, showing the first four sutures, from phylembryonic to the paranepionic substage. 9, from side; 10, from front.

Figs. 11, 12. Larval stage, diameter of 0.92 mm., first whorl, showing first eight sutures, and transitions from the metanepionic (*Anarcestes* stage), through paranepionic (*Tornoceras* stage) to ananeanic (*Prionoceras*) stage. 11, from front; 12, from side.

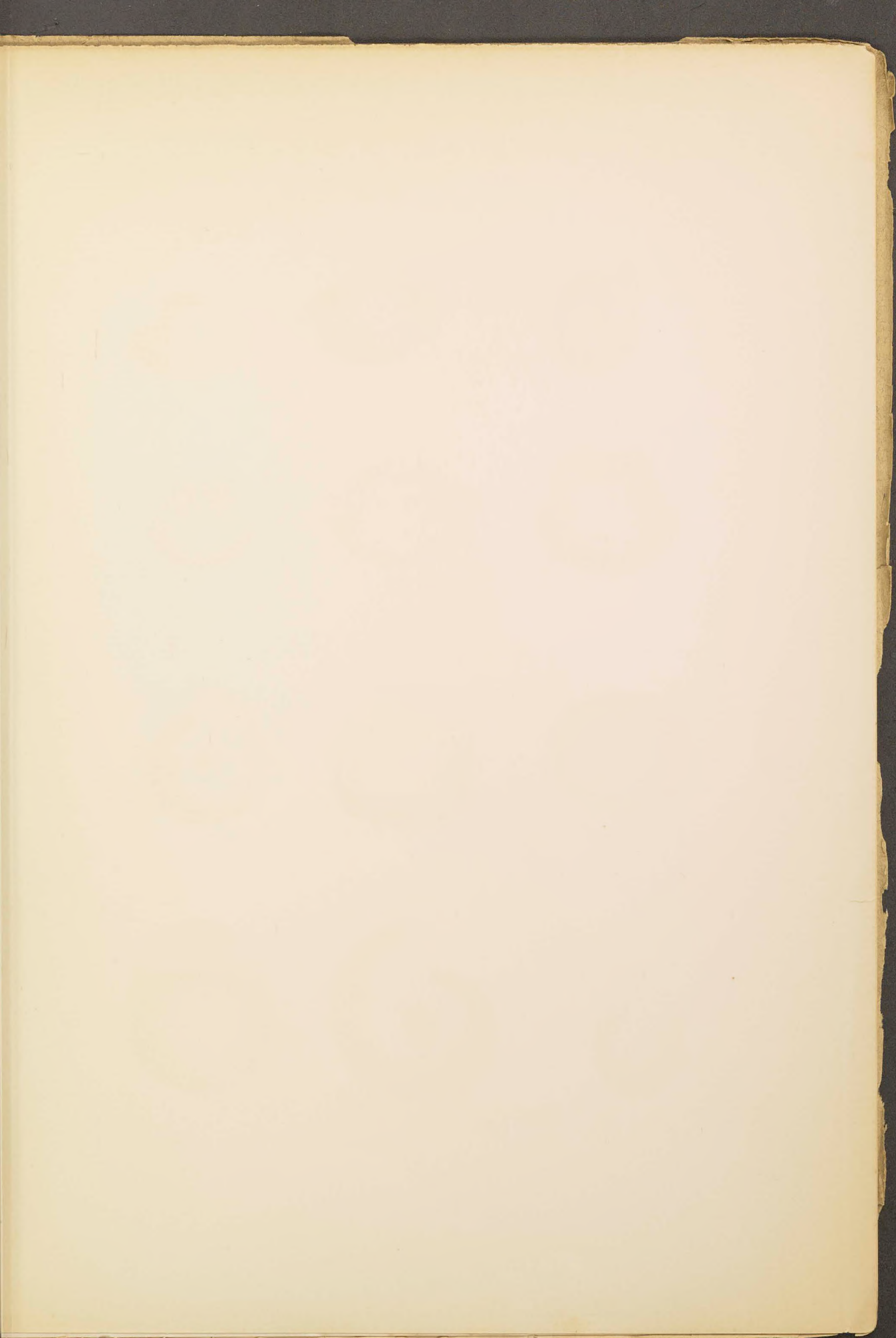














## EXPLANATION OF THE FIGURES.

## PLATE XIV.

All figures on this plate are twenty times enlarged, except fig. 9, which is twice natural size.

*Glyphioceras incisum* HYATT.

Figs. 1, 2. Adolescent stage, one and three-fourths whorls, diameter of 1.29 mm., last whorl is ananeanic (*Prionoceras* stage) and shows transition from paranepionic. 1, front; 2, side.

Figs. 3, 4. Adolescent stage, diameter of 1.37 mm., one and seven-eighths whorls, *Prionoceras* stage. 3, from front; 4, from side.

Figs. 5, 6. Adolescent stage, diameter of 1.64 mm., two and one-eighth whorls, *Prionoceras* stage. 5, from front; 6, from side.

Figs. 7, 8. End of adolescent stage, diameter of 2.25 mm.; two and three-fourths whorls; transition from *Prionoceras* to *Glyphioceras* in the division of the ventral lobe, and beginning rounding of the whorl. 7, side view; 8, front view.

Fig. 9. Early adult stage, diameter of 15 mm., twice enlarged.





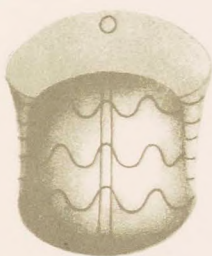
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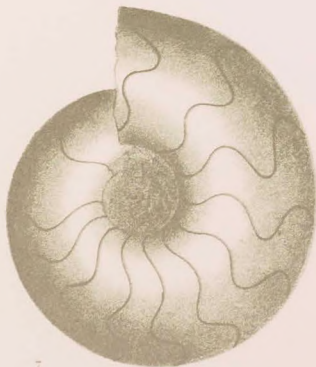
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## EXPLANATION OF THE FIGURES.

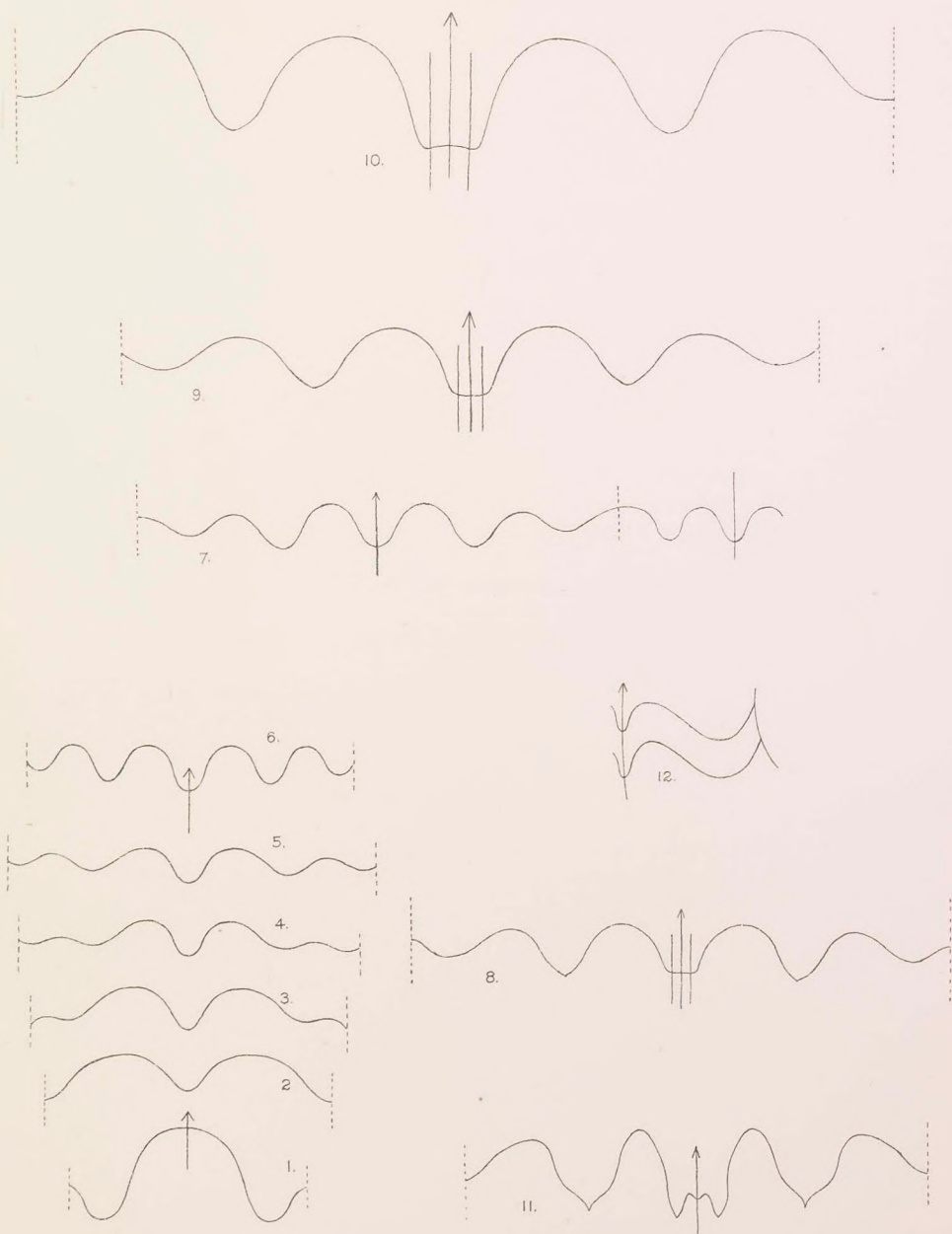
## PLATE XV.

All figures of *Glyphioceras* on this plate are magnified forty times, except fig. 11, which is four times enlarged.

*Glyphioceras incisum* HYATT.

- Fig. 1. First suture, ananepionic.  
Fig. 2. Second suture, metanepionic (*Anarcestes*).  
Fig. 3. Third suture, metanepionic.  
Fig. 4. Fourth suture, paranepionic (*Tornoceras*).  
Fig. 5. Fifth suture, at one-half a revolution, and diameter of 0.74 mm., paranepionic.  
Fig. 6. Eighth suture, at one revolution, and diameter of 0.92 mm., ananeanic (*Prionoceras*).  
Fig. 7. Suture at one and three-fourths revolutions, and diameter of 1.29 mm., ananeanic.  
Fig. 8. Sutures at one and seven-eighths revolutions, and diameter of 1.37 mm., (*Prionoceras*).  
Fig. 9. Sutures at two and one-eighth revolutions, and diameter of 1.64 mm., (*Prionoceras*).  
Fig. 10. Sutures at diameter of 2.25 mm.,  $2\frac{3}{4}$  whorls, transition from *Prionoceras* to *Glyphioceras*.  
Fig. 11. Sutures at diameter of 15 mm., adult.  
Fig. 12. Sutures of *Anarcestes subnautilus*, after L. von Buch, Gesamte Werke, Vol. IV, p. 116, Pl. XI, fig. 9.

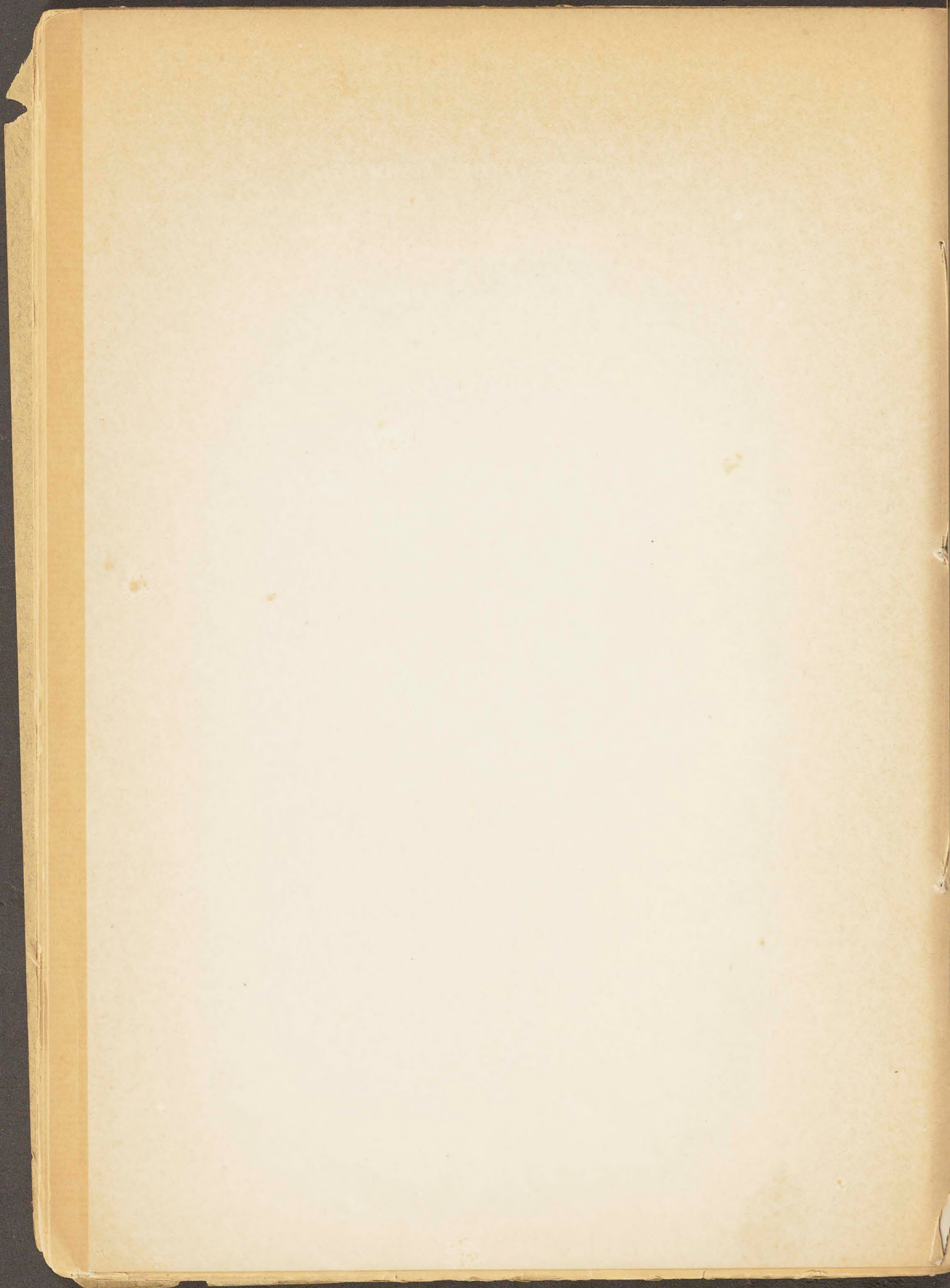




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